STUDIES OF HUMAN TWINS.

II. Asymmetry Reversal, of Mirror Imaging in Identical Twins.

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Introduction.

One of the most striking phenomena observed among monozygotic twins is that of the reversal of asymmetry between the individuals of a pair. Among armadillo quadruplets the present writer (Newman, 1916) found numerous instances in which a band or scute doubling occurred on the left side of one twin and on the right side of the other. Such cases call to mind the fact that in human double monsters (Siamese twins) *situs inversus viscerum* occurs in many cases. The same type of asymmetry reversal was noted by Swett and by Morrill in double-headed fish embryos. In separate identical twins in man it has been noted that the incidence of left-handedness in one twin of a pair is very much greater than among fraternal twins or in the general population of single individuals. Asymmetry reversal in the direction of crown whorl of the head hair seems to have about the same incidence in monozygotic twins, dizygotic twins, and single individuals as has left-handedness. These two expressions of asymmetry have been studied intensively in the present investigation and their significance will be discussed in some detail later.

Handedness an Expression of Asymmetry.

As an introduction to this study it seems well to examine the phenomena of handedness as it is found among human beings. In the first place, there are two distinct kinds of handedness: that which is genetically determined and that which is the result of twinning and therefore epigenetically determined.

Genetic handedness is evidently transmitted in such a way that any given zygote will give rise, when no twinning occurs, to a right-handed or left-handed single individual. There seems, however, to be varying degrees of right- or left-handedness. The majority of individuals, apparently about eighty per cent.

of single individuals, are definitely righ-handed; about four per cent. definitely left-handed, and the remaining sixteen per cent. partially left-handed or ambidextrous. The incidence of right- and left-handedness is about what one would expect if right-handedness is a dominant Mendelian unit character and left-handedness recessive. The ambidextrous individuals and those showing lesser degrees of left-handedness may be heterozygous individuals in which the dominance of right-handedness is incomplete.

The other type of left-handedness, quite different in origin and heritability, is that which results epigenetically as the result of the twinning. Such left-handedness, being a somatic modification would not be hereditary: it would be merely an expression of asymmetry reversal due to the development of a whole individual from a half embryo which had already become more or less differentiated in a left-handed direction before the separation into twins has taken place.

Thus in genetic right-handed embryos which undergo twinning after some asymmetry has been established, the left-hand half embryo would be the superior one and would give rise to a right-handed individual, since right-handed superiority is due to left-sided superiority in the brain. Conversely, in a genetic left-handed embryo, the right side would be superior and the left side the inferior side, in which case the left-handed individual would retain the genetic asymmetry and the right-handed individual would exhibit asymmetry reversal.

In embryos genetically ambidextrous the right and left sides would be equal and would produce twins both of whom would be ambidextrous.

Previous Data on Handedness in Twins.

A good deal of attention has been paid by various authors to the peculiar incidence of left-handedness in twins. Siemens (1924) found in thirty-seven pairs of identical twins twenty-six cases both right-handed, ten cases in which one was right-handed and the other left-handed, and one case where both were left-handed. In a later paper the same writer reported on a larger number of identical twins (the total number not given) in which

there were twenty-one cases where one was right- and the other left-handed and three cases where both were left-handed.

Weitz (1924) found among eighteen pairs of identical twins, seven pairs composed of a right- and a left-hander, ten pairs both right-handed, and one pair both left-handed.

Dahlberg (1926) reports for sixty-nine pairs of identicals fifty-three pairs both right-handed, twelve pairs one left-handed, and four pairs both left-handed. Adding the three sets of cases together, we have one hundred and twenty-four cases of identical twins divided as follows:

89 pairs, both right-handed,	71.8	per cent.
29 pairs, one left-handed,	23.4	per cent.
6 pairs, both left-handed,	4.8	per cent.

Dahlberg has also studied the incidence of left-handedness in one hundred and twenty-eight pairs of dizygotic twins. The following figures indicate his results:

111 pairs, both right-handed,	86.7	per cent.
16 pairs, one left-handed	12.5	per cent.
1 pair, both left-handed,	0.8	per cent.

It will be seen that the incidence of left-handedness among identical twins is over twice as great as among fraternal, or four times as great in proportion to the number of zygotes involved, for a pair of identical twins involves only one zygote. Even among fraternal twins, the incidence of left-handedness is relatively high as compared with the general population, which is reported by Jones (1918) to be about four per cent. Jones' estimate, however, is probably much too low and takes account of only the most complete cases of left-handedness.

Lauterbach (1925) reports among fifty-seven same-sexed twins (not distinguished as to monozygotic or dizygotic origin) twenty pairs in which one was left-handed, about 35 per cent. of all cases. This is a higher incidence of left-handedness than any previously reported, especially when it is taken into consideration that the group examined consists of both identical and fraternal twins.

The most recent data on handedness in twins is furnished by Verschuer (1927). He found one or more left-handed individuals in 26.8 per cent. of seventy-nine pairs of identical twins and

in 26.3 per cent. of the thirty-eight pairs of fraternal twins. They were distributed as follows:

Identical Twins.	*Fraternal Twins.*
58 both right-handed.	28 both right-handed.
15 one right- the other left-handed.	10 one right- the other left-handed.
5 both left-handed.	0 both left-handed.
1 one right-handed, the other ambidextrous.	

The percentage is rather low as compared with those of others, particularly those of Lauterbach and the present writer, but the difference is probably due to the inclusion of only the cases of complete left-handedness. The percentage of pairs showing left-handedness among fraternal twins is exceptionally high and not in accord with the findings of others. Possibly the relatively small number of cases may be the cause of this discrepancy. Even more probable, it seems to me, is the inclusion among fraternal twins of a few of the least similar identical twins among whom left-handedness is common.

Criteria of Handedness.

It is by no means a simple matter to diagnose left-handedness. There are many cases, of course, where the twins are (or were at an earlier period) obvious left-handers, but there are also many cases where congenital left-handedness is obscured by training the right hand and suppressing the left. Such cases often result in a sort of ambidextrality in ordinary manipulations. In our work we have used as a test of handedness speed in tapping with wrist and fingers. In all cases of complete left-handedness the tapping tests confirm the left-handed diagnosis. It appears to be safe then to use the tapping tests to reveal native left-handedness obscured by right-hand training or various degrees of partial left-handedness.

A good many cases of partial left-handedness were revealed by tapping tests. Among identical twins, in addition to the eleven pairs showing complete left-handedness, there were thirteen pairs (both of whom considered themselves right-handers) in which some degree of left-handed superiority was revealed in one or both members of the pair. In three of these pairs both members

were shown to be partially left-handed, and in two pairs both members were definitely ambidextrous.

Among fraternal twins, in addition to six pairs in which one individual was completely left-handed, there were five pairs in which one individual was partially left-handed, two pairs in which both were partially left-handed, and two pairs in which one individual was right-handed and the other ambidextrous.

Assuming that all these cases represent grades of left-handedness we have added to the seventeen pairs showing complete left-handedness twenty-two pairs showing partial left-handedness, a total of thirty-nine out of one hundred pairs in which some degree of left-handedness appears in one or both members of a pair. This high percentage would be much like that found by Lauterbach (35 per cent.) if we omitted the cases of ambidextrality.

Crown Whorl an Expression of Asymmetry.

As is well known, the head hair at the crown twists or whorls in either a clockwise or a counter-clockwise direction. The great majority of individuals show clockwise hair-whorl, and therefore clockwise asymmetry may be considered as the normal and counter-clockwise asymmetry as the reversed asymmetry. Various writers have called attention to sporadic instances of reversed crown whorl, and a few cases have been described for identical twins.

Only one writer, however, has thus far made a systematic study of crown whorl in twins. Lauterbach (1925) in a study of resemblances and differences in twins has presented some very interesting data. Out of fifty-seven pairs of same-sexed twins there occurred fifteen pairs in which one or both twins showed counter-clockwise hair-whorl. In one of these cases both twins were counter-clockwise. This means that about twenty-six per cent. of the pairs of same-sexed twins showed asymmetry reversal in hair-whorl. In addition to these, there were six cases showing double crown in which one half of the whorl has a clockwise and the other a counter-clockwise direction. These cases are possibly comparable to ambidextrality in handedness and should probably be listed as a form of asymmetry reversal. Adding these six cases, the percentage of pairs showing more or less reversed hair-whorl among same-sexed twins comes to nearly

37 per cent., not unlike the percentage of left-handedness in the same set of twins, which was 35 per cent.

In our own collection of one hundred pairs of same-sexed twins there are in all ninety-five pairs in which it was possible to determine the hair-whorl. In five pairs (three identicals and two fraternals) the kinky or closely matted character of the hair rendered diagnosis of hair-whorl extremely difficult or impossible. Among the identicals there were twenty pairs showing some form of asymmetry reversal in crown-whorl. In fifteen pairs one twin showed clockwise and the other counter-clockwise whorl, in three pairs both twins were counter-clockwise, and in one pair one twin had a double crown and the other a clockwise whorl. The remaining twenty-seven diagnosed pairs showed clockwise hair whorl in both twins.

Among fraternal twins there were but five pairs having any form of asymmetry reversal in hair-whorl. In four of these pairs, one twin was counter-clockwise, and in one pair one twin had a double crown and the other a clockwise whorl.

As in the case of handedness, there are doubtless instances of incomplete asymmetry reversal that are not recognizable. Probably some of the crowns diagnosed as slightly clockwise or indefinite may be cases of partial asymmetry reversal.

Crown-whorl has one advantage over handedness as a criterion of reversal of asymmetry in that it is not subject to modification by training and is therefore a somewhat surer sign of asymmetry reversal than is left-handedness.

The Relation between Handedness and Crown Whorl.

In only ten pairs of our identical twins do we find reversed asymmetry of any sort (either left-handedness, counter-clockwise hair-whorl, or both) in both twins of a pair. In eight of these cases (73, 25, 23, 87, 43, 38, 7, 27) both twins of a pair are left-handed or both have counter-clockwise hair whorl. It would seem natural to assume that all such pairs have been derived from zygotes, genetically left-handed. But what shall we do with the other two cases (13 and 72) in which one twin of each pair is plainly left-handed and the other clearly counter-clockwise in hair whorl? Since both of these indications are valid

criteria of reversed asymmetry there seems no escape from the conclusion that these two pairs also are derived from genetically left-handed zygotes.

The Incidence of Asymmetry Reversal in Our Own Collection of Twins.

When the present study began, the writer was keenly on the lookout for evidences of asymmetry reversal in identical twins. The expectation was that the more strikingly identical the twins were, the more evidence of asymmetry reversal would be present. Before the study was half over it seemed certain that this expectation was not to be realized. In fact, the very opposite of this appeared to be true, namely, that the least evidence of asymmetry reversal appears among those twins that are practically indistinguishable, while the twins that are less nearly identical show the most evidence of reversal of asymmetry.

In order to test out this conception, the writer tried to arrange the fifty pairs of identical twins in the order of their closeness of resemblance, including resemblances in features, height, weight, headsize, finger prints and palm prints. After this was done, Mrs. Blythe Mitchell, the one who has had the most intimate and prolonged acquaintance with the twins, was asked to rearrange the cases according to her impression as to the degrees of identity. On the whole, there was a very close agreement, no case being changed more than a few places up or down in the series. Using the photographs, we worked over all cases together and arrived at the arrangement shown in Table I., which is not intended to be exact, place for place, but certainly represents a real grouping in the sense that the first five pairs are more similar than the second five, the second five than the third, the ninth five than the tenth. Within groups of five the order might be more or less shifted as the criteria of resemblance are not entirely objective, but depend to a large extent upon one's judgment of degrees of facial resemblance. In the following table asymmetries in handedness, crown-whorl, and head dimensions are given for the fifty pairs arranged in fives, beginning with the most alike and ending with the least alike. In this table *R* and *L* indicate definite right- and left-handedness, *l* indicates partial left-handedness,

A indicates ambidextrality; + indicates clockwise, or the common type of hair-whorl; and — indicates counter-clockwise hair-whorl. Double hair-whorls are indicated by (+ —).

TABLE I.

Serial No.	Twin.	Sex.	Handedness.	Crown Whorl.	Head Length.	Size Breadth.	Remarks.
62	A	♂	R	+	17.4	15.5	
	B	♂	R	+	17.2	15.2	
98	A	♀	R	+	17.7	13.9	
	B	♀	R	+	17.5	14.1	
63	A	♂	R	+	18.2	14.3	
	B	♂	R	−	18.1	13.9	
40	A	♂	R	(+ −)	17.85	15.0	
	B	♂	R	+	18.1	15.5	
3	A	♂	R	?	20.0	14.75	Negroes. Crown-whorl could not be made out.
	B	♂	R	?	19.7	14.3	
9	A	♀	R	−	17.0	13.6	A shows partial asymmetry reversal in crown.
	B	♀	R	+	17.7	13.7	
80	A	♀	R	+	18.7	13.5	
	B	♀	R	+	18.1	13.2	
67	A	♂	R	+	18.9	14.6	
	B	♂	l	+	18.7	14.1	B left-handed in wrist tapping.
55	A	♂	R	+	19.2	14.8	
	B	♂	R	+	19.1	14.4	
35	A	♂	R	−	18.55	15.0	A shows partial asymmetry reversal in crown.
	B	♂	R	+	18.55	15.1	
96	A	♂	R	−	18.10	13.9	
	B	♂	R	+	18.15	13.9	
* 73	A	♀	l	−	17.1	13.35	A, incompletely reversed crown; left-handed in finger tapping.
	B	♀	A	−	17.5	13.5	B, completely reversed in crown; nearly ambidextrous.
102	A	♀	R	−	17.8	15.0	
	B	♀	R	+	18.1	15.0	
* 25	A	♂	R	−	18.3	14.2	
	B	♂	R	−	17.9	13.9	
30	A	♀	R	+	18.8	13.7	
	B	♀	R	+	18.7	13.55	

TABLE I. (*Continued.*)

Serial No.	Twin.	Sex.	Handedness.	Crown Whorl.	Head Length.	Size Breadth.	Remarks.
* 23	A	♀	A	+	16.2	14.25	A more left-handed than B.
	B	♀	A	+	16.1	14.0	
94	A	♀	R	+	18.4	13.5	
	B	♀	L	+	18.15	13.2	
68	A	♀	R	−	17.45	14.25	
	B	♀	R	+	17.5	14.4	
49	A	♀	l	−	18.0	14.6	
	B	♀	R	+	18.2	14.1	
* 13	A	♀	R	−	17.0	14.5	
	B	♀	L	+	17.0	14.6	
78	A	♂	L	+	18.45	14.7	
	B	♂	R	+	18.40	14.7	
* 87	A	♂	A	−	19.95	13.9	A more decidedly left-handed.
	B	♂	A	+	19.7	14.0	
* 43	A	♂	l	−	19.6	15.7	Bats left-handed naturally.
	B	♂	l	+	19.1	15.3	Left-handed in finger tapping.
* 38	A	♀	l	−	19.4	15.5	Left in both wrist and finger tapping.
	B	♀	l	−	19.1	15.5	Left in finger tapping only.
79	A	♂	R	+	17.35	13.9	
	B	♂	L	+	18.1	13.3	
* 72	A	♂	L	+	19.15	14.5	
	B	♂	R	−	19.25	15.0	
99	A	♂	R	+	18.2	14.5	
	B	♂	R	+	18.25	14.5	
33	A	♂	L	+	18.05	14.9	
	B	♂	R	+	18.05	15.25	
53	A	♂	R	+	19.0	13.9	
	B	♂	L	+	18.8	13.4	
44	A	♂	L	+	18.5	14.3	
	B	♂	R	+	19.5	13.9	
2	A	♀	L	?	17.45	14.45	
	B	♀	R	?	17.95	14.35	
91	A	♀	R	+	18.0	13.8	
	B	♀	R	+	17.9	13.9	
100	A	♂	R	+	17.65	13.6	
	B	♂	R	+	17.2	14.0	

TABLE I. (*Continued.*)

Serial No.	Twin.	Sex.	Handedness.	Crown Whorl.	Head Length.	Size Breadth.	Remarks.
101	A	♂	R	+	18.6	15.5	
	B	♂	L	+	18.9	15.5	
70	A	♂	R	+	18.5	15.6	
	B	♂	L	+	18.1	15.3	
37	A	♂	R	+	19.15	14.75	
	B	♂	l	+	19.35	14.65	Slightly left-handed in wrist tapping.
34	A	♂	R	+	18.8	14.8	Inclined to be ambidextrous.
	B	♂	l	+	19.0	14.8	Slightly left-handed in finger tapping.
28	A	♀	R	−	16.8	13.8	
	B	♀	R	+	17.7	13.9	
*7	A	♂	l	−	17.3	15.7	Strongly left-handed in finger tapping.
	B	♂	l	+	17.6	15.5	Strongly left-handed in finger tapping.
6	A	♀	R	+	17.5	13.9	
	B	♀	R	+	17.2	13.7	
97	A	♀	R	+	17.85	16.0	
	B	♀	R	+	18.0	16.0	
17	A	♀	R	+	17.85	14.45	
	B	♀	R	+	17.75	14.65	
14	A	♀	R	−	17.2	14.45	
	B	♀	R	+	17.45	14.45	
15	A	♂	R	+	19.65	14.6	Both ambidextrous as babies.
	B	♂	R	−	19.45	14.9	
69	A	♂	R	+	18.75	14.9	
	B	♂	R	+	18.9	14.3	
24	A	♂	R	+	17.45	14.65	
	B	♂	l	+	17.4	14.65	Slightly left-handed in playing marbles.
18	A	♂	R	+	18.6	13.8	
	B	♂	R	+	18.8	13.8	
*27	A	♂	R	−	19.25	13.5	
	B	♂	l	−	19.3	13.7	Slightly left-handed in wrist and finger tapping.
41	A	♀	L	?	17.26	15.2	Hair whorl could not be determined.
	B	♀	R	?	17.6	15.6	
60	A	♀	R	+	17.6	14.1	
	B	♀	l	+	17.5	14.15	Slightly left-handed in finger tapping.

Handedness in Relation to Degrees of Resemblance.

In this table there are listed twelve pairs of twins one member of which is fully left-handed and, in addition to these, there are eleven cases that show partial left-handedness in one or both individuals of the pair. Besides the twenty-three cases showing some degree of left-handedness, there are two cases in which both members of the pair are classed as ambidextrous. Thus in exactly fifty per cent. of our pairs of identical twins there is some degree of left-handedness.

It is significant that the first case in the series to show complete left-handedness is seventeenth out of fifty. There are only two cases of partial left-handedness among the fifteen most strikingly similar set of twins, while some degree of left-handedness becomes the rule rather than the exception from the sixteenth to the end of the list.

Crown Whorl in Relation to Degrees of Resemblance.

The incidence of asymmetry reversal in crown hair whorl follows the same general lines as does left-handedness. In the first ten pairs there is but one case (No. 63, in third place) that shows true counter-clockwise hair-whorl. Two other cases (No. 9, in sixth place, and No. 35, in tenth place) show a mixed hair-whorl partly clockwise and partly counter-clockwise. There is also one case of a double hair-whorl, one whorl being clockwise, the other counter-clockwise (No. 40, in fourth place). The most frequent incidence of counter-clockwise hair-whorl in one twin occurs among the middle grade twins, neither the most alike or the most different. This is true also of left-handedness, and such a correspondence in the incidence of two forms of asymmetry reversal must have some real significance.

The Relation between Handedness and Head Size.

In the following study both left-handedness and counter-clockwise hair-whorl are taken to be equivalent criteria of either genetic or epigenetic reversal of asymmetry. For the present we shall omit from consideration the ten pairs of twins (Nos. 73, 25, 23, 13, 87, 43, 38, 72, 7 and 27) that were diagnosed as derived from zygotes genetically left-handed. These are starred in the list.

Before discussing the relation of head-size to handedness it should be said that there is undoubtedly some inaccuracy in the figures for head dimensions. Repeated measurements of the same head rarely give exactly the same result. Dahlberg has calculated that the average error in head measurements is about 0.5 mm. It seems probable that our own errors were at least as great as this, and probably greater. Hence differences of no more than 1 mm. may be ignored or considered as without significance.

Glance with me down the list of forty pairs of identical twins not previously diagnosed as derived from genetically left-handed zygotes. In all, there are seventeen pairs in which one twin may be classed as right-handed, the other left-handed, and in which there is a significant difference in head size. In thirteen of these pairs (63, 9, 67, 102, 68, 33, 53, 44, 2, 70, 28, 14 and 41) the right-handed individual, derived from the superior side of the embryo, has a distinctly larger head.

The four other cases (49, 79, 101 and 34) reverse this condition, the left-hander has the larger head, though case 34 is ambiguous in that one twin is slightly left-handed in tapping and the other nearly ambidextrous and may therefore belong with the list of ten diagnosed as derived from a left-handed zygote. The other three cases (49, 79 and 101) are valid exceptions. Let us consider these cases carefully. What would happen in the case of a genetically left-handed zygote if one of the twins underwent asymmetry reversal? Obviously the reversed twin would be a right-hander, and should have the smaller head. This interpretation appears to fit cases 49, 79 and 101. It would be strange if some cases such as these did not occur in view of the existence of genetically left-handed zygotes.

This hypothesis, that head size is correlated with handedness, may be checked still further by examining the ten pairs of twins diagnosed as derived from genetically left-handed zygotes. Of these, eight show a significant difference in head size. These eight cases deserve individual attention:

Pair No. 73.—This is a confusing case. Twin A shows left-handedness in finger tapping and has a partially reversed hair-whorl; twin B is practically ambidextrous in tapping and has a well-defined counter-clockwise hair-whorl, the only really posi-

tive indication of left-handedness present in the pair. This twin (B) has the larger head.

Pair No. 25.—In this pair both twins are right-handed and both have counter-clockwise hair-whorl. It is impossible to decide which of these has been derived from the superior side or whether they are derived from a right-handed or left-handed zygote, for the handedness and hair-whorl completely contradict each other.

Pair No. 23.—Both twins are ambidextrous, and both have clockwise hair-whorl. Twin A, with the larger head, is more nearly left-handed than B.

Pair No. 87.—Twin A, while ambidextrous, tends to be more left-handed than B, and has counter-clockwise hair-whorl; twin B is ambidextrous and has clockwise hair-whorl. Evidently A is the left-handed (superior) individual, and he has the larger head.

Pair No. 43.—Both twins are partly (probably natively) left-handed. Twin A has counter-clockwise hair-whorl, twin B clock wise. A, the more distinctly left-handed twin, has the larger head.

Pair No. 38.—Both twins are partially left-handed and both have counter-clockwise hair-whorl. A is left-handed in both wrist and finger tapping; B, only in finger tapping. A, the more left-handed, has the larger head.

Pair No. 72.—Twin A is strongly left-handed but has clockwise hair-whorl; twin B is right-handed but has counter-clockwise hair-whorl. It is impossible to say which individual should be diagnosed as from the superior side, since the two criteria seem to be of equal value. Of the two the reversed hair-whorl is somewhat safer as a criterion, and it happens that the twin (B) with the counter-clockwise hair-whorl has the larger head.

Pair No. 27.—Twin A is right-handed; B, slightly left-handed in wrist and finger tapping. Both have counter-clockwise hair-whorl. Twin B, the partially left-handed member of the pair, has the larger head.

All of these eight cases except pair 25, which is neutral, support the conclusion that the twin derived from the genetically superior side (the right side in these cases) of the embryo has the larger head.

One other class of cases remains to be dealt with, those in which a significant difference in head size exists without any complete

asymmetry reversal in handedness or hair-whorl. There are nine such pairs (62, 3, 80, 55, 30, 6, 97, 69, 18). In all but two of these cases (3, 55, 30, 6, 97, 69, 18) one twin was definitely more right-handed than the other and the more right-handed individual has the larger head in all pairs. In pairs 62 and 80, both twins are equally strongly right-handed and offer neutral evidence. Instead of weakening the general theory, then, all of these cases, where varying degrees of difference in right-handedness but no true left-handedness occur, tend strongly to support it. There is beyond question a strong correlation between handedness and head size. With very few exceptions indeed, the twin having the larger head shows evidence of having been derived from the genetically superior side of the embryo; from the left-hand side in twins derived from zygotes genetically destined to form right-handers, and from the right side of zygotes destined to form left-handers.

Twinning and the Asymmetry Mechanism.

The data just presented have given rise to a theory that seems to rationalize for the first time the peculiar incidence of reversal of asymmetry in twins. It is well known that in some groups of animals, notably those characterized by a striking degree of determinate cleavage, bilateral symmetry and asymmetry are established in the undivided zygote before or at the time of the first cleavage. In those forms, on the other hand, that show a strong tendency toward indeterminate cleavage, notably the vertebrates and echinoderms, symmetry and asymmetry are not definitely fixed until considerably later in development. The writer's work (Newman, 1924) on asymmetry reversal in the starfish indicates clearly that asymmetry is fixed before the time of gastrulation, for no reversal of asymmtry could be induced in embryos older than late blastulæ.

There are also indications among the vertebrates that asymmetry is established prior to or during gastrulation. Thus in the nine-banded armadillo, the only case of twinning among mammals where the stage at which twinning occurs is definitely known, it has been found that the first step in the twinning process usually precedes the period at which symmetry and asymmetry are es-

tablished and that the second step in twinning takes place during the process of the establishment of the axis of symmetry. By analogy, we may infer that twinning in man takes place in close association with, and possibly as an aberration of, the process of establishing and fixing the relations of symmetry and asymmetry in the embryo.

Now, since no biologic processes takes place with the same clock-like precision in all specimens, we may suppose that the twinning act in some cases is consummated during relatively early stages of the establishment of symmetry and asymmetry, and that in other cases it is established later. In the cases in which twinning occurs relatively late, the establishment of a single bilateral individual may have gone so far that complete twinning is impossible. This is probably the case in all partial twinning, resulting in conjoined twins and double monsters. In such twins one of the most striking features is the occurrence of profound reversal of asymmetry, as expressed in more or less complete *situs inversus viscerum*.

If then, we may assume that conjoined twins with the most extreme reversal of asymmetry in the inferior component, represents one end of the series of twins, it is natural to assume that the opposite end of the series is represented by cases in which twinning is consummated before any asymmetry is fixed. In such cases the twins would be derived from two equivalent primordia which had not yet been differentiated into right- and left-hand sides. When, later, asymmetry comes to be established in these two genetically equivalent and still undifferentiated embryos, it should follow the same course in both and each should develop the same asymmetry as the embryo would have done had it not undergone twinning. Thus, if the original embryo was genetically a right-hander, two right-handed twins should result; similarly, if the original embryo was genetically a left-hander, two left-handed twins should result—a condition not uncommon among twins, but hitherto unexplained. In such twins we would expect a high degree of same-sided asymmetry in such details as palm and finger prints, ear shape, dentition, handedness, hair-whorl, etc. Moreover, since the two twins are derived from two primordia that have not yet become differentiated as right- and

left-hand components, the two resulting twins would be expected to be very strikingly similar, more similar than would be twins separated after asymmetry had been more or less fixed in the embryo from which they are derived.

Thus the earlier twinning occurs with respect to the establishment of asymmetry, the more similar should be the resultant twins and the less should they show such evidences of reversal of asymmetry as left-handedness and counter-clockwise hair whorl. This explains why these criteria of asymmetry reversal are rarely present in the most strikingly similar twins and are increasingly common among identical twins that are less similar.

If this theory be sound, and there is much evidence in its favor, we have discovered another mechanism, not classifiable as environmental, that operates to make identical twins different. This factor, the asymmetry mechanism, may be the main, if not the only, factor responsible for observed differences between identical twins reared together. Consequently it would be quite unsafe to infer that any differences between such twins are due to differences in environment or in training. On the other hand, once we have established the average degree of difference between identical twins reared together, we should be able to use this as a base line in determining to what extent, in cases of identical twins reared apart, the differences in environment have operated to increase the physical or mental difference.

This theory goes far to explain why some, but not all, pairs of twins show left-handedness and counter-clockwise hair-whorl in one twin of a pair; why there should be occasional cases in which both twins of a pair are left-handed or have counter-clockwise hair-whorl; why there should be various degrees of incomplete asymmetry reversal as the result of separation of twins prior to complete establishment of asymmetry. The establishment of asymmetry is a progressive process and takes some time to become fully fixed. Hence we may expect to find that twinning early in the process will result in little if any signs of asymmetry reversal in one of the twins, and that twinning occurring late in the process will result in extensive reversal of asymmetry in one of the components.

In brief, this theory seems to clear up many if not all the

formerly baffling asymmetry situations found in twins. It lacks experimental confirmation, but this must be so from the nature of the material. Yet the data themselves almost speak out the theory of their own accord.

Summary.

1. Reversal of asymmetry in monozygotic twins expresses itself in varying degrees, ranging from complete *situs inversus viscerum* in conjoined twins to left-handedness or counter-clockwise hair-whorl in separate twins.

2. There are two kinds of handedness: genetic and epigenetic. Genetic right- and left-handedness have about the incidence, respectively, of dominant and recessive allelomorphs. Epigenetic left-handedness (or in genetic left-handers, right-handedness) results from twinning, the inferior side having an asymmetry opposite to that of the superior side.

3. Arranging fifty pairs of identical twins in the order of their closeness of physical resemblance, it is found that there is very little evidence of asymmetry reversal among the most similar twins, while the less similar twins show a high degree of it.

4. Clockwise hair-whorl has about the same incidence as right-handedness, and counter-clockwise hair-whorl that of left-handedness.

5. Varying degrees of partial left-handedness and of ambidextrality are revealed by tapping tests.

6. Ten pairs of identical twins show asymmetry reversal in both members of a pair and are therefore diagnosed as derived from genetically "left-handed" zygotes; three pairs showing asymmetry reversal in but one twin should probably be classed as "left-handers"; the remaining thirty-seven pairs are believed to be derived from right-handed zygotes.

7. There is a very close correlation between head size and handedness. The twin derived from the superior side of the embryo nearly always has a significantly larger head.

8. The reason why many but not all identical twins show asymmetry reversal in one twin is that the epigenetic establishment of asymmetry takes place sometimes before and sometimes after twinning. If it takes place before twinning the twins will show

a high degree of asymmetry reversal; if it takes place after the twinning the twins will both show the same asymmetry and be in other respects more alike than when the establishment of asymmetry precedes twinning; if it takes place during the twinning process the twins will show varying degrees of asymmetry reversal in one individual and varying degrees of close resemblance in physical and mental characters.

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